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CAPTORHINID REPTILES FROM THE EARLY PERMIAN OF NEW MEXICO, WITH DESCRIPTION OF A NEW GENUS AND SPECIES

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ABSTRACT

A new genus and species of single-tooth-rowed captorhinid, *Rhiodenticulatus heatoni,* is based on two skulls and partial postcranial skeletons collected from the Lower Permian Cutler Formation near Arroyo de Agua, north-central New Mexico. A cladistic analysis of its relationships to other single-tooth-rowed captorhinids suggests that it is a primitive sister taxon to *Labidosaurus* and *Eocaptorhinus.* The dentition of *R. heatoni,* however, exhibits several unique derived features which are interpreted as representing an adaptation to a specialized diet.

Puercosaurus obtusidens Williston, 1916, the only previously described captorhinid from New Mexico, is declared a *nomen dubium* because the holotypic left dentary is indeterminate, and there is no basis for accepting that it and the two poorly preserved captorhinid skulls found at a different locality and referred to the species by Williston (1916) are conspecific. Additional captorhinid remains have been collected recently from the Lower Permian Cutler, Abo, and Sangre de Cristo formations at widely scattered localities in central and northern New Mexico. Though these specimens, as well as the skulls referred to "*Puercosaurus obtusidens,*" are too poorly preserved to be assigned to existing or new taxa, they do indicate that the Captorhinidae was diverse and widely distributed in the Lower Permian of New Mexico.

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1

INTRODUCTION

Published accounts of captorhinid reptiles from the late Paleozoic of New Mexico have been limited to two reports (Williston, 1916; Langston, 1953). Williston (1916) described a small captorhinid, *Puercosaurus obtusidens,* on the basis of three poorly preserved and incomplete specimens, a left dentary and two skulls, collected from the Cutler Formation in the Rio Puerco drainage in the north-central part of the state. Further discoveries of captorhinids were not made until 1934–1935, when collecting was resumed by field parties from the University of California, Berkeley. While conducting extensive field work in the Lower Permian Cutler Formation of the same area, three moderately well preserved specimens, including two skulls with jaws and articulated postcranial materials were found at the well known Camp quarry near the small village of Arroyo de Agua (see Langston, 1953, for histories and vertebrate assemblages of well known localities of the area). The only published report of these specimens was a brief reference to them by Langston (1953) in a discussion of the age of the late Paleozoic vertebrate-bearing strata of New Mexico. Here he notes (1953: 410) "a small romeriid cotylosaur possibly referable to *Puercosaurus obtusidens* is more primitive than *Romeria texana* of the middle Wichita (Putnam)" of the Lower Permian of Texas. Extensive collecting by the authors during the past several years in the Lower Permian deposits throughout New Mexico has resulted in the discovery of additional captorhinid remains from the Cutler, Abo, and Sangre de Cristo formations.

Taxonomic evaluation of the undescribed captorhinid materials of New Mexico has necessitated a reexamination of the type specimens of *Puercosaurus obtusidens* Williston (1916). The partial left dentary, designated by Williston as the holotype, is not only indeterminate, but also provides no basis for considering it conspecific with the two partial, crushed skulls referred by him to the species. Even though the two referred skulls are undoubtedly captorhinids, they are too poorly preserved to be assigned to an established or new taxon. Under these circumstances *P. obtusidens* is judged a *nomen dubium.* On the other hand, the specimens collected by the University of California, Berkeley, are sufficiently well preserved and unique to be referred to a new genus and species, *Rhiodenticulatus heatoni.* With the exception of the types of this species, all other Lower Permian captorhinid specimens from New Mexico are too incomplete to recommend assignment to existing or new taxa. Yet, they exhibit sufficient variation to indicate that the group was probably quite diverse and widely distributed in New Mexico during the Early Permian.

Throughout the text the abbreviations CM, FMNH, and UCMP are used to refer to collections of the Carnegie Museum of Natural History, Field Museum, Chicago, and the Museum of Paleontology, University of California, Berkeley, respectively.

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Order Cotylosauria
Suborder Captorhinomorpha
Family Captorhinidae
Genus *Puercosaurus* Williston, 1916
Puercosaurus obtusidens Williston, 1916, *nomen dubium*

Puercosaurus obtusidens Williston, 1916:189–192, fig. 37A–D.

Remarks. —The original description of *Puercosaurus obtusidens* Williston (1916) was based on poorly preserved and incomplete specimens—an incomplete dentigerous left dentary, FMNH 743, designated as the holotype and two severely crushed skulls, FMNH 745, referred to the species (Fig. 6; only one of the skulls is figured). Williston (1916) illustrated the mandible and one of the two skulls, but a partial reconstruction of the skull was based on both skulls. Although the specimens were collected from the Lower Permian Cutler Formation near Arroyo de Agua in the Rio Puerco drainage area, north-central New Mexico, the holotypic dentary is from the well known Miller bonebed (see Langston, 1953, for description of locality), whereas the referred skulls were apparently found at least several kilometers away along the Rio Puerco (Williston, 1916). The holotypic dentary is too poorly preserved and incomplete to be reasonably certain that it belongs to that family. Further, the holotypic dentary and referred skulls do not exhibit any unique features in common which would demonstrate that they are conspecific. In view of these circumstances *P. obtusidens* is declared here a *nomen dubium*. Though the skulls FMNH 745 are sufficiently complete to recognize their captorhinid affinities, assignment to either a known or new species is not possible.

Genus *Rhiodenticulatus,* new genus

Type species. —*Rhiodenticulatus heatoni,* new species.

Etymology. —From the Greek *rhio,* nose, and *denticulatus,* with small teeth, referring to the relatively small teeth of the premaxilla.

Diagnosis. —Small captorhinid that differs from all other single-tooth-rowed captorhinids in the following features: 1) premaxillary dentition reduced to three teeth which are subequal in size and equal to or smaller than precanine maxillary teeth; 2) reduction of maxillary dentition to 11 teeth; 3) number of precanines reduced to two; 4) extremely large
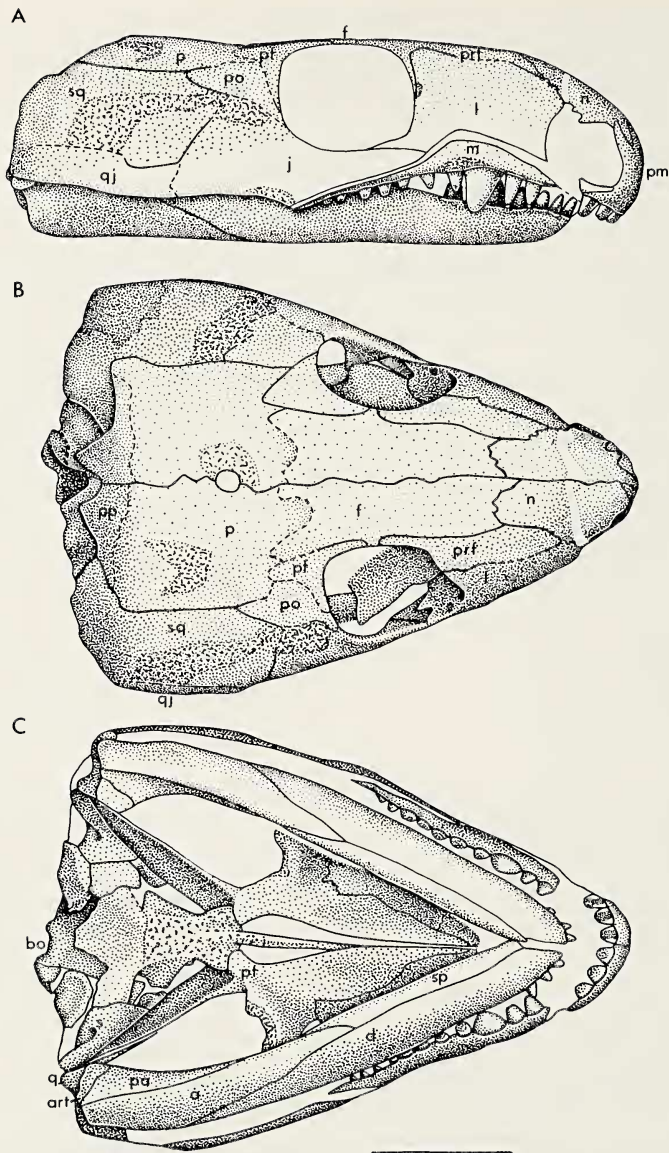
Fig. 1.—*Rhiodenticulatus heatoni,* holotype, UCMP 35757. Skull in A, lateral, B, dorsal, and C, ventral views. Abbreviations: a, angular; art, articular; bo, basioccipital; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pa, prearticular; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sp, splenial; sq, squamosal. Scale = 1 cm.

single canine with basal diameter as much as twice that of any post-canine; 5) very broad lacrimal with a height (measured at the highest level of the dorsal expansion of the maxilla) to length (shortest distance between orbit and naris) ratio of .65 to .73; and 6) prefrontal extends far anteriorly to a level about 84 to 90% of the distance from the orbit to the naris. Distinguished from *Labidosaurus* and *Eocaptorhinus* by its proportionately narrower skull postorbitally. Straight occipital margin of skull table separates it from *Romeria* which has a bilateral parietal embayment and from *Labidosaurus* and *Eocaptorhinus* which have a median embayment. Differs from *Romeria* and *Protocaptorhinus* in having a long, low rectangular quadratojugal with a longitudinal length that is approximately four times the height. Pointed postcanine teeth of *Rhiodenticulatus heatoni* are distinguishable from the blunt teeth of *Labidosaurus* and *Eocaptorhinus*.

Rhiodenticulatus heatoni, new species

Etymology.—Named in honor of the late Malcolm J. Heaton in recognition of his significant contributions to our understanding of the morphology and phylogenetics of the Captorhinidae.

Holotype.—UCMP 35757: partial, articulated skeleton that includes skull with closely joined lower jaw, vertebral series with ribs from the axis to the seventh caudal, pectoral and pelvic girdles, right humerus and proximal ends of ulna and radius, femora, left tibia, fibulae, and tarsi; skull not attached to postcranial skeleton.

Paratypes.—UCMP 40209: skull with closely joined lower jaw, missing left postorbital cheek region and posterior half of left mandible.

UCMP 40210: partial, articulated postcranial skeleton preserved in three small segments: 1) a series of seven postaxial cervical and dorsal vertebrae with ribs, essentially complete pectoral girdle, and proximal ends of humeri; 2) series of six vertebrae that includes the last two presacrals, two sacrals with ribs, and the first two caudals, and pelvis; and 3) portion of the left hindlimb, including proximal two thirds of femur and nearly complete tibia. It is quite likely that UCMP 40209 and UCMP 40210 belong to the same individual.

Horizon and locality.—All specimens are from the Cutler Formation exposures of the Rio Puerco drainage, Rio Arriba County, north-central New Mexico. An Early Permian Wolfcampian age is generally accepted for these exposures. Although the holotype and paratypes are listed as coming from UCMP Camp quarry locality V-2814, Langston (1952: 98) notes that they were probably not found in the main bone level of the quarry, but rather as float on the slope of Loma Salazar a few feet away and presumably at or just above the quarry bone level. The Camp quarry is located in SW1/4NE1/4NE1/4 sec. 8, T. 22 N., R. 3 E., about
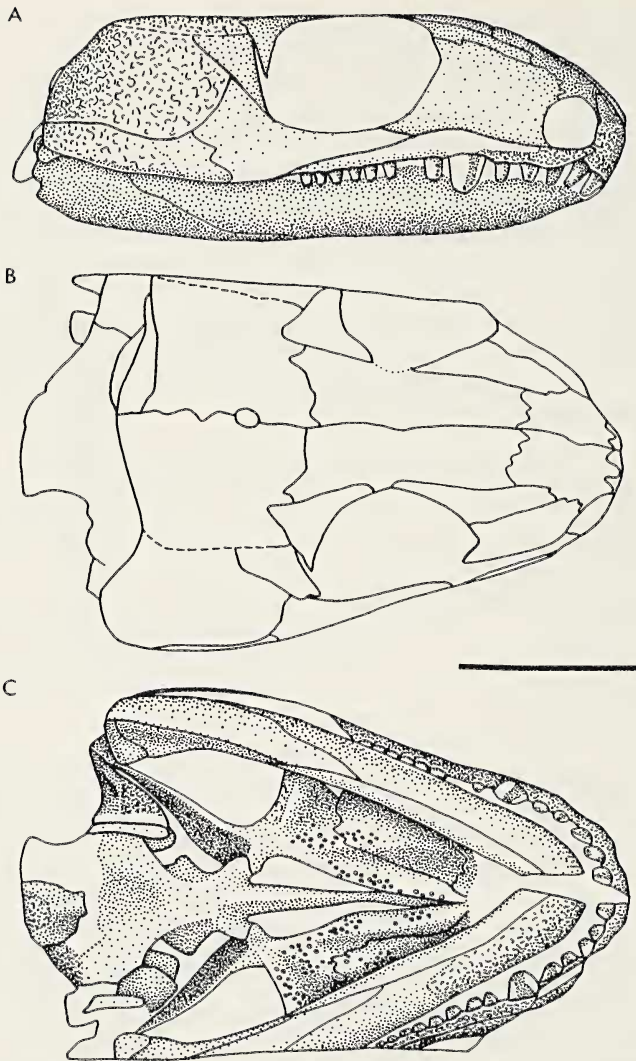
Fig. 2.—*Rhiodenticulatus heatoni,* paratype, UCMP 40209. Skull in A, lateral, B, dorsal, and C, ventral views. Scale = 1 cm.

1.1 km southeast of Arroyo de Agua. All three specimens are preserved in red, indurated concretionary nodules.

Description

Skull.—Specimens of *Rhiodenticulatus heatoni* exhibit the general structural pattern seen in all captorhinids and, therefore, aside from a

few structures, Figs. 1, 2 eliminate the need for a detailed description of its anatomy. The skulls of the holotype UCMP 35757 and paratype UCMP 40209 have suffered little distortion, but most of the superficial features of the skulls, such as sculpturing, have been lost due to weathering and excessive preparation performed prior to this study. In UCMP 40209 the left postorbital region was removed in the late 1930s in an attempt to study the braincase in thin section. The extent of ossification of the appendicular and axial portions of the holotypic skeleton suggests that it is a mature individual. The skulls are triangular, with the postorbital width being only about 80 to 82% of the midline length. The occipital margin of the skull stable is straight.

The downturned premaxilla possesses three teeth. In the paratype UCMP 40209 (Fig. 2A) the anterior end of the right maxilla greatly overlaps the lateral surface of the maxillary process of the premaxilla, making it appear as though the third premaxillary tooth originates from the anterior end of the maxilla. Although imperfectly preserved, the premaxillary teeth obviously had the shape of sharply pointed pegs, were subequal in size, and were approximately the same size as, or even possibly slightly smaller than, the precanine maxillary teeth. Anteriorly the maxilla forms the ventral rim of the naris, gradually expands to a moderate midlength dorsal swelling, and then tapers to a posterior terminus at, or just short of, the level of the posterior margin of the orbit. The right and left maxillae of the holotype possess 10 and 11 teeth, respectively, whereas both maxillae of UCMP 40209 possess 11. In both skulls the third tooth forms an extremely large canine relative to any of the other marginal teeth, with a basal diameter equal to, or greater than, twice that of any of the postcanines. In the holotype the precanines are slightly larger than the largest postcanines. The postcanines exhibit a steady decrease in size posteriorly. As in the premaxilla, the maxillary teeth have the form of sharply pointed pegs. In neither skull is it possible to observe directly that only a single row of marginal maxillary teeth is present. Indirect evidence for a single row is present, however, in that the teeth form a straight row along the outermost margin of the jaw, the postcanines exhibit a steady decrease in size, and there does not appear to be sufficient space for an additional tooth row on the alveolar shelf of the maxilla.

The lacrimal is unusual in being very broad. The ratio of its height (measured at the level of the dorsalmost expansion of the maxilla) to length (measured as the shortest distance between the orbit and naris) is about .65 in the holotype and about .73 in UCMP 40209. There is a correspondingly narrower lateral exposure of the prefrontal as a result of the expanded height of the lacrimal. The prefrontal is also very long and extends anteriorly along the dorsal margin of the lacrimal to a level that is about 90 and 84% of the distance between the orbit and the naris in the holotype and UCMP 40209, respectively. A long ventral

process of the prefrontal can be seen in the holotype extending along the medial margin of the lacrimal on the anterior orbital rim. The prefrontal and postfrontal are separated by only a small lateral process of the frontal on the dorsal rim of the orbit. The frontals have a long, narrow rectangular outline. Measured from the level of their orbital contribution, the length of the anterior portion of the frontal is almost one and one half times that of the posterior portion. The pineal opening in both skulls is large and positioned anterior of the midlength of the union of the parietals. The supratemporals are not preserved in either skull. The presence of the postparietal is indicated only in the holotype and then only as an impression of its ventral surface; its suture with the parietal is therefore uncertain. The anterior ends of the right jugals of both skulls appear to wedge between the lacrimal and maxilla, rather than forming the step-like sutural encroachment onto the lateral surface of the dorsal margin of the maxilla seen in other captorhinids (Heaton, 1979). This is undoubtedly due to imperfect preservation, however, inasmuch as the standard condition is present on the nonfigured left side of the holotypic skull. The quadratojugal has the outline of a long, low rectangle, with the length exceeding the height by about four times.

Description of the palate is limited by the attached jaws. As in all captorhinids there is no ectopterygoid, and the rectangular palatine probably extends posteriorly to the subtemporal fossa. The presence of a medial jugal process cannot be determined. The denticle fields of the palate are preserved only in the paratype UCMP 40209. There is a scattering of denticles along the posterior border of the transverse flange of the pterygoid. There are also two faint, denticle bearing ridges; one extends along the medial border of the palatal ramus of the pterygoid, and a second extends obliquely anterolaterally across the palatal ramus of the pterygoid and onto the palatine. The three columns of irregularly arranged denticles converge toward the basicranial articulation. Denticles also appear to be present on the parasphenoid.

The braincases of the holotype and UCMP 40209 are exposed in ventral and occipital views and, though poorly preserved for the most part, do not appear to exhibit any noteworthy differences from the standard captorhinid construction. Both stapes of the holotype and the right of UCMP 40209 are exposed in ventral view and are well enough preserved to deserve comment. Though the footplates are not fully exposed, they appear to conform closely to those of *Ecocaptorhinus* (Heaton, 1979) and *Captorhinus* (Fox and Bowman, 1966). It has the form of a broadly oval disk that thins toward its periphery. The disk is drawn out posterolaterally into a cone-like structure, with the apex being smoothly continuous with the columella. The cross-sectional shape of columella, which remains unchanged throughout its short length, is that of a mediolaterally flattened blade having a vertical height

about three times its horizontal width. A large stapedial foramen pierces the proximal end of the columella at a slightly anteromedial angle from the vertical. Occipital view of the holotypic skull (not drawn) clearly reveals the dorsal process of the left stapes just distal to the stapedial foramen. It is very narrow, tapers to a point distally, and curves slightly medially.

The mandibles of both skulls are visible in partial lateral view and in ventral view; their sutural pattern and shape show no deviation from those of other captorhinids. The posterior ends of the mandibles are too damaged to determine whether or not a retroarticular process was present. Dentary teeth are visible only in the holotype, but unfortunately only the anterior half of the series is visible, and these are only partially exposed. The first three teeth exhibit a marked increase in size posteriorly, with the third tooth probably being the largest of the entire series. On the basis of basal diameter, the fourth and fifth teeth are slightly smaller than the third, whereas the sixth appears to be equal to the third in size. The seventh and eighth decrease further in size, as undoubtedly does the remaining unexposed portion of the series. It is estimated that the dentary of the holotype held 14 or 15 teeth.

Postcranial skeleton. — Whereas the skull of *Rhiodenticulatus heatoni* exhibits notable differences from those of other captorhinids, the opposite appears to be true of the postcranial skeleton; this is not unexpected inasmuch as this characterizes the history of captorhinids (Heaton and Reisz, 1980).

The holotype appears to possess a complete, articulated vertebral column from the axis to the sixth caudal vertebra (Fig. 3). Unfortunately, the column is exposed only in ventral view, and small segments of the series are hidden by the pectoral and pelvic girdles. Despite this, it can be safely estimated that the entire presacral column consisted of 25 vertebrae. The centra are slightly pinched laterally, and except for what is believed to be the axial centrum the ventral midlines are still broadly rounded in transverse section; the axial centrum has a distinct keel-like ventral midline. The wing-like transverse processes exhibit a gradual reduction in their lateral extent posteriorly in the column. The ventral surface of the processes slope anteroventrally, and the lateral width narrows as the processes extend to the anterior rim of the centrum. Both ends of the centra are slightly beveled to accommodate the intercentra, giving them a slightly keystone appearance in lateral view. The intercentra are variably displaced dorsally into the notochordal canals of the centra, where attempts to fully expose them would result in damage to the centra. As a result, many of the intercentra appear to be absent, whereas those that are partially exposed vary in size and have a lozenge-shaped outline. The first chevron occurs between caudals three and four.
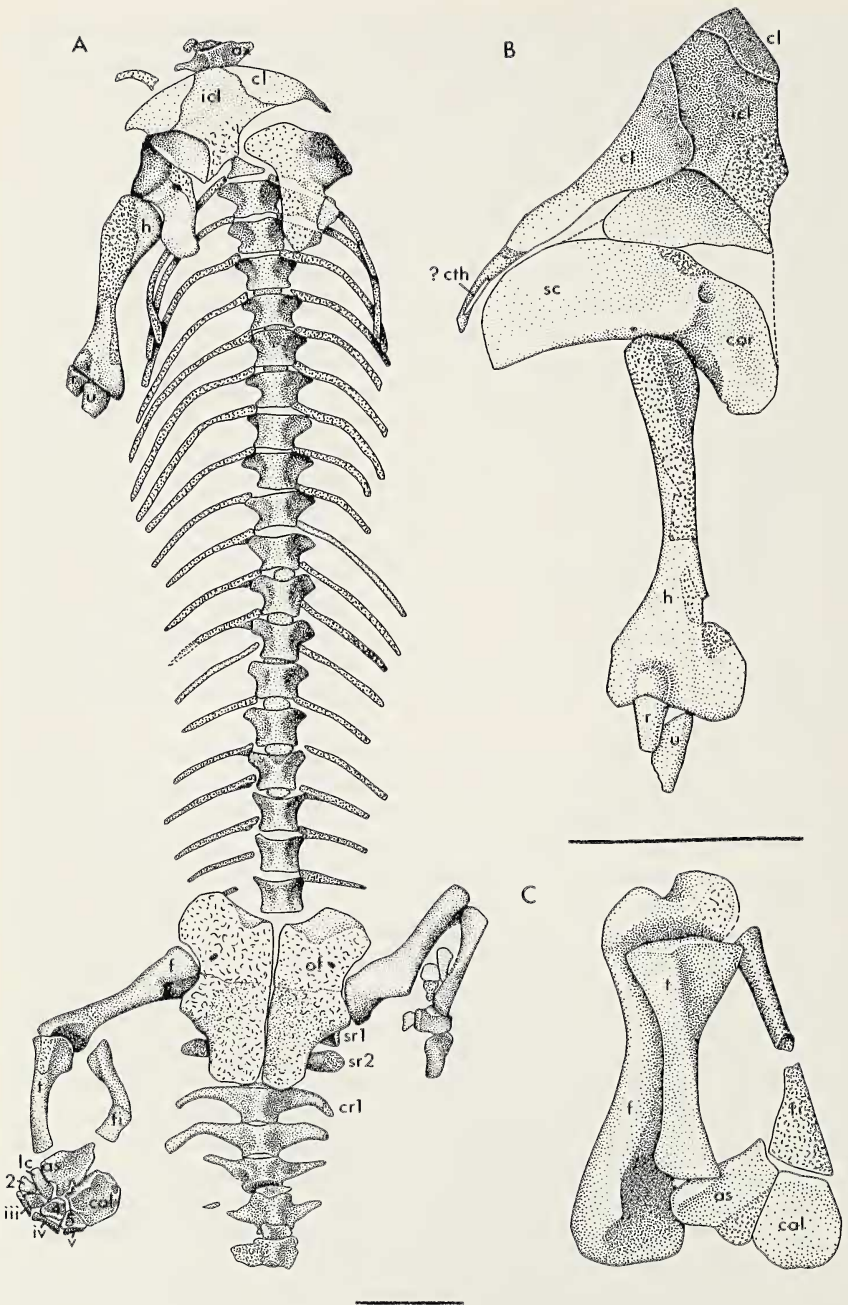
The string of seven postaxial cervical and dorsal vertebrae of UCMP 40210 are exposed in dorsal view only (Fig. 4A) and undoubtedly include postaxial cervicals. Although poorly preserved, the neural arches exhibit the swollen appearance so typical of captorhinids. The neural spines are barely developed and appear as mere nubbins. The zygapophyses are widely spaced from the midline, giving the neural arches the typical lateral expansion of captorhinids. The transverse processes extend laterally beyond the zygapophyses. Only the badly weathered neural arches are exposed in the UCMP 40210 vertebral series which includes the second to last presacral to the second caudal (not figured), and they reveal no important differences from the far anterior presacral of the same specimen.

The ribs of the holotype and paratype UCMP 40210 are moderately well preserved, but the expansion of the heads is rarely visible, and the shafts frequently appear as narrow rods. The heads of the postaxial cervical ribs appear to be holocephalous and articulate in part with the intercentra. The rib shafts of the cervicals of UCMP 40210 are expanded into blade-like structures, whereas the more posterior rib shafts of the holotype are subcircular in cross-section. The ribs of the anterior half of the presacral column are more strongly curved posteroventrally than those of the posterior half. The sacral ribs are straight, thick, and greatly expanded distally. The anterior caudal ribs of the holotype are fused to the centra, curve strongly posteriorly, are thicker than the presacral ribs, and quickly decrease in length more posteriorly in the column.

The greater portions of the pectoral girdles are preserved in both the holotype and paratype UCMP 40210, and together they exhibit most of the important features of this structure (Figs. 3A, B, 4B). The head of the interclavicle is roughly diamond-shaped, and the long, thin stem is nearly complete in UCMP 40210, missing only a small part of the distal end. The ventral plates of the clavicles are not complete, but impressions on the interclavicles indicate that they were broad and met medially; there is also no indication of a prominent, thumb-like posterior process diverging from the main body of the ventral plate as has been described in *Labidosaurus* (Williston, 1917) and *Captorhinus* (Holmes, 1977). The narrow dorsal stem is directed abruptly dorsally

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Fig. 3.—*Rhiodenticulatus heatoni,* holotype, UCMP 35757. A, ventral view of postcranial skeleton, B, right lateral view of shoulder region, and C, lateral view of left hindlimb. Abbreviations: as, astragalus; ax, axis; cal, calcaneum; cl, clavicle; cor, coracoid; cr, caudal rib; cth, cleithrum; f, femur; fi, fibula; h, humerus; icl, interclavicle; lc, lateral centrale; of, obturator foramen; r, radius; sc, scapula; sr, sacral rib; t, tibia; u, ulna; 2, 4, 5, distal tarsals; iii, iv, v, metatarsals. Scales = 1 cm.
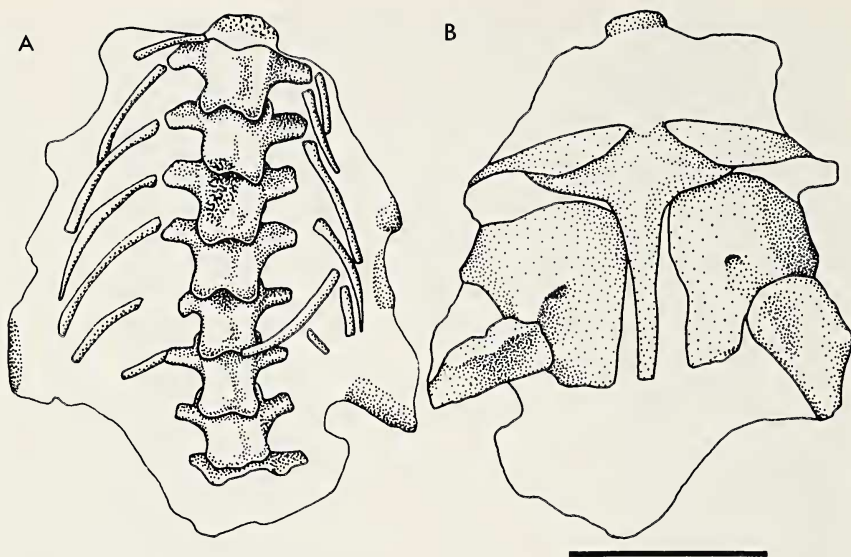
Fig. 4.—*Rhiodenticulatus heatoni,*paratype, UCMP 40210. A, dorsal view of series of seven far anterior presacral vertebrae with ribs, and B, ventral view of pectoral girdle with proximal ends of humeri preserved in a single nodule.

at nearly a right angle to the ventral plate. As in *Captorhinus* (Holmes, 1977), a distinct, posteriorly directed flange-like expansion of the ventral half of the dorsal stem for the clavicular deltoid muscle is clearly seen in the holotype. What may be a portion of the cleithrum is present on the distal end of the dorsal stem of the right clavicle of the holotype. There are no visible sutural divisions of the endochondral portion of the pectoral girdle. The scapular blade curves dorsally rather abruptly from the essentially horizontal coracoid plate. The anterior and posterior margins of the scapular blade are essentially straight and parallel to each other except for the anterodorsal corner being broadly curved. The anterior coracoid portion expands a short distance anteriorly beyond the scapular blade as a smoothly rounded plate. A coracoid foramen located ventromedially to the anterior buttress of the glenoid and a supraglenoid foramen on the posterior margin of the lateral surface of the scapular blade just above the supraglenoid buttress are clearly visible in the holotype and UCMP 40210.

Essentially all that is visible of the pelves of the holotype and UCMP 40210 is the worn ventral surface of the puboischiadic plate (Fig. 3A); the less complete pelvis of UCMP 40210 is not figured. In both specimens osssification along the puboischiadic suture appears to be complete in that there are no open spaces. The sutural division between

the pubis and ischium is barely discernable in the holotype. The anterior border of the puboischiadic plate is moderately concave. The ischium is slightly longer and narrower than the pubis. A short distance from the ventral rim of the acetabulum the pubis is perforated by the obturator foramen.

The humerus is best represented in the holotype (Fig. 3A, B). It is poorly preserved, but exhibits the same general configuration as those of *Captorhinus* and *Eocaptorhinus* except that the shaft and distal head have a more slender appearance. Its length, about 1.8 cm, is approximately 90% of that of the femur. All other forelimb elements are either too incomplete to comment on or are absent. The hindlimb and pes are preserved only in the holotype (Fig. 3A, C). The preservation of the femora allows recognition of only some of the major features of this element. Except in being considerably more slender, particularly the shaft, the femur is very similar to that of *Captorhinus*. It is about 2.0 cm long, has a minimum shaft diameter of about 1.3 mm, and a maximum width of the distal head of 4.3 mm. The head appears rather massive, with a well developed intertrochanteric fossa. The popliteal area is a smooth, broadly concave depression. Though the internal trochanter is well developed, there appears to no distinct step or notch between it and the head. The tibiae and fibulae of the holotype are present, but only those of the left limb are well preserved. The tibia and fibula appear to be identical to those of *Captorhinus* except in being noticeably more slender. In typical primitive reptilian fashion the tibia is much shorter, 11.0 mm, than the femur, roughly 55% of its length. The mediolateral width of the massive proximal end is about 45% of the length, whereas anteroposterior width of the distal end is about 36% of the length; the narrowest mediolateral width of the shaft is about 0.8 mm. A deep groove divides the anterior face and articular surface of the expanded proximal end; the groove is bounded medially by a prominent cnemial crest. The lateral margin of the tibia is bowed slightly medially away from the fibula. The left fibula is about 12.3 mm long and the mediolaterally expanded proximal and distal ends are about 2.5 and 3.5 mm wide, respectively; the narrowest mediolateral width of the shaft is about 1.1 mm. The medial margin of the fibula is strongly concave and the lateral margin only very slightly convex, giving it the appearance of being bowed laterally away from the tibia.

The tarsi of the holotype are well ossified. The right, exposed in ventral view (Fig. 3A), is nearly complete, missing only the first distal tarsal, whereas the left is represented only by the dorsally exposed calcaneum and astragulus (Fig. 3C). The tarsal elements conform closely to the pattern seen in *Captorhinus* (Peabody, 1951) except for two apparent deviations; the fourth distal tarsal is relatively smaller and

the fifth which is relatively larger than in *Captorhinus*. The typical pattern in primitive reptiles is for the fourth distal to be considerably larger than the other distal tarsals. In *Rhiodenticulatus,* however, the fourth distal is roughly equal in size to the fifth. The extreme proximal ends of the third, fourth, and fifth metatarsals are all that remains of the rest of the right pes.

DISCUSSION

Placement of *Rhiodenticulatus heatoni* within the Captorhinidae of the suborder Captorhinomorpha is unquestionable. It should be made clear, however, that we follow Heaton (1979), Gaffney and McKenna (1979), Reisz (1980), and Heaton and Reisz (in press) in the assignment of genera in the two recognized captorhinomorph families, the Early Pennsylvanian to Early Permian Protorothyrididae (=Romeriidae of many authors) and Early to Late Permian Captorhinidae. The captorhinids are differentiated from the protorothyridids by their low, wide, massive skull, hooked premaxillae, loss of tabulars and ectopterygoids, fully ossified paroccipital processes, stoutly built postcranial skeleton, 25 presacral vertebrae with swollen neural arches and low neural spines, absence of cleithra, thumb-like process on the ventral plate of clavicle, short stoutly built limbs, absence of a supinator process of humerus, and wide manus and pes. Presently, about 14 genera of captorhinids are recognized. Among these, however, only four genera, *Romeria, Protocaptorhinus, Eocaptorhinus,* and *Labidosaurus,* could conceivably be confused with *Rhiodenticulatus,* because they possess single-rowed, marginal dentitions.

Clark and Carroll (1973) and Heaton (1979) presented nearly identical phylogenies in which the series of successively later occurring, single-tooth-rowed captorhinids *Romeria, Protocaptorhinus,* and *Eocaptorhinus* forms a single, continuous, phylogenetic lineage depicting transitional morphological stages that links the protorothyridids with the later occurring, multiple-tooth-rowed *Captorhinus.* Among the captorhinids with multiple-rowed marginal dentitions, *Captorhinus* is the only genus known in great detail and is also generally accepted as the most primitive. *Labidosaurus,* the least understood of the single-tooth-rowed captorhinids, is not included in Heaton's (1979) phylogenetic scheme, but is depicted in Clark and Caroll's (1973) phylogenetic tree as the end member of an offshoot from *Protocaptorhinus.* Gaffney and McKenna (1979:7) criticized the systematic methodology used by Clark and Carroll, and Heaton as being "stratophenetic" (*sensu* Gingerich, 1976) in which "similar morphologies are arranged stratigraphically and connected using usually implicit rather than explicit criteria, to form what are interpreted as ancestor-descendant lineages."

Gaffney and McKenna, without altering the basic phylogenies of Clark and Carroll, and Heaton, reexpressed them in the form of a cladogram and, thus, as a testable hypothesis. Our only serious reservation of their cladogram of the Captorhinidae is the position of *Labidosaurus* as a member of the clade containing *Protocaptorhinus*. As brought out below, *Labidosaurus* shares with *Eocaptorhinus* and *Captorhinus* several derived features of the skull not seen in *Protocaptorhinus*. Further, restudy of *Labidosaurus* is greatly needed before its phylogenetic reltionships can be accurately evaluated. Despite this, the cladogram of Gaffney and McKenna presents a reasonable understanding of the evolutionary relationships of the captorhinids and, along with the detailed morphological studies of the known captorhinomorphs by Carroll and Baird (1972), Clark and Carroll (1973), Heaton (1979), and Olson (1984), provides a basis for assessing the polarity of several character states of *Rhiodenticulatus heatoni.*

The maxillary dentitions of the holotype and paratype UCMP 40209 of *Rhiodenticulatus* are unique among the single-tooth-rowed captorhinids in possessing: 1) a single, extremely large canine whose basal diameter is equal to, or greater than, twice that of any of the postcanines; 2) 11 teeth; and 3) two precanines. It can also be noted that among the protorothyridids only the Pennsylvanian *Cephalerpeton* exhibits a similar specialization toward a greatly reduced number (16) of maxillary teeth that includes a low number (four) of precanines (Reisz and Baird, 1983). Protorothyridids typically possess, as does *Romeria,* a pair of prominent, subequal canines, yet their basal diameters are far less than twice that of the largest postcanines. Although a single tooth may be designated as a canine in *Protocaptorhinus* and *Labidosaurus,* it is not as prominent as either of the paired canines of *Romeria. Eocaptorhinus* also exhibits a single, prominent canine, and although the first through third postcanines may be noticeably shorter, their basal diameters are only slightly smaller than that of the canine. In the holotypic skull of *Rhiodenticulatus,* having a midline length of about 38 mm, the basal diameter of the canine is about 2.2 mm. This is larger in both absolute and relative measurements than the canines of *Romeria* and *Protocaptorhinus,* in which the basal diameters range from roughly 1.2 to 1.7 mm for skulls 50 to 53 mm in midline length. On the other hand, though the maximum basal diameter of the canines in *Eocaptorhinus* and *Labidosaurus* may be as much as 2.6 and 3.0 mm, respectively, their midline skull lengths are as much as two and four times greater than that of *Rhiodenticulatus.*

Previous authors (Clark and Carroll, 1973; Heaton, 1979) have noted that there is a general reduction in the number of maxillary teeth in successively later occurring, single-tooth-rowed captorhinids. Approx-

imate maxillary tooth counts for *Protorothyris, Romeria, Protocapto-rhinus, Labidosaurus,* and *Eocaptorhinus* are 24–30, 22–23, 18–22, 14–18, and 17–22, respectively. The maximum of 11 maxillary teeth in *Rhiodenticulatus* can only be interpreted as a unique derived character. Probably related to this trend is the unique occurrence in *Rhiodentic-ulatus* of only two precanines. Protorothyridids typically possess five precanines, but as many as seven or eight have been described in *Paleothyris* (Carroll, 1969). A further slight reduction in the number of precanines occurs in the successively later occurring captorhinids; *Romeria prima* possesses six precanines, *R. texana, Protocaptorhinus,* and *Labidosaurus* four or five, *Eocaptorhinus* three or occasionally four, and *Captorhinus* three or rarely four.

The lacrimal of *Rhiodenticulatus* may be unique among all capto-rhinomorphs in having an unusually large height to length ratio. The height was measured at the level of the dorsalmost expansion of the maxilla, whereas the length was taken as the shortest distance between the orbit and naris. Despite the small errors expected in making these sorts of measurements, the height to length ratios of .65 and .73 for the holotype UCMP 35757 and paratype UCMP 40209, respectively, are considerably greater than those of other single-tooth-rowed cap-torhinids, which range from about .25 to .40. In the protorothyridids *Paleothyris* and *Protorothyris,* the lacrimals are very long and narrow, and have a height to length ratio of about .17. The fact that in *Rhio-denticulatus* the ratio is smaller for the larger holotype than for the paratype, suggests that the ratio decreases somewhat with growth or increase in size. This notion is reinforced in *Romeria texana,* where the ratios for an adult and juvenile described by Clark and Carroll (1973) are .27 and .40, respectively.

The extreme anterior extent of the prefrontal along the dorsal margin of the lacrimal in *Rhiodenticulatus* also sets it apart from all other captorhinids. In the holotype UCMP 35757 and paratype UCMP 40209 the prefrontal extends anteriorly to a level that is 90 and 84% of the distance from the orbit to the naris, respectively, whereas in other captorhinids and in *Protorothyris* this measurement ranges from ap-proximately 43 to 58%. It might be suspected that the greater anterior extension of the prefrontal in *Rhiodenticulatus* is due to removal, either as a result of weathering or mechanical preparation, of that portion of the nasal overlying its anterior end. In *Eocaptorhinus,* for example, where additional exposure of the prefrontal could conceivably increase its preorbital length by as much as 28% (Heaton, 1979), the anterior extension of the prefrontal would increase from about 44 to 56% of the distance between the orbit and naris. As pointed out by Heaton (1979), in Clark and Carroll's (1973) illustration and reconstruction of

the holotype of *Romeria texana* the prefrontals appear unusually long due to the exposure of that portion of their anterior ends normally overlapped by the nasals. For this reason we used Heaton's (1979) reconstruction of *Romeria texana* in calculating the relative anterior extension of the prefrontal. In the holotype and paratype UCMP 40209 of *Rhiodenticulatus* both pairs of prefrontals have identical lateral exposure configurations, strongly suggesting that they have not been significantly distorted in this way by weathering or excessive preparation.

Rhiodenticulatus exhibits several shared derived features with other advanced single-tooth-rowed captorhinids. Its possession of only three premaxillary teeth is considered advanced among the captorhinids in view of the general trend within the captorhinomorphs toward reduction in the number of premaxillary teeth. Protorothyridids typically have five or six premaxillary teeth, although *Protorothyris archeri* appears to have four and *Cephalerpeton* only three (Reisz and Baird, 1983). Premaxillary tooth counts for *Romeria prima, R. texana, Protocaptorhinus, Labidosaurus,* and *Eocaptorhinus* are 4, 5, 4 or 5, 3, and 4 or 5, respectively. The premaxilla of *Captorhinus* typically possesses four teeth and rarely three or five. *Rhiodenticulatus* is also similar to the more derived captorhinids *Labidosaurus, Eocaptorhinus,* and *Captorhinus* in having a long, narrow, rectangular quadratojugal in which the longitudinal length exceeds by almost four times the height, and the dorsal margin tends to be straight. As pointed out by Heaton (1979), in the more primitive *Romeria* and *Protocaptorhinus* the dorsal margin of the quadratojugal tends to be more convex. Heaton also noted that in the reconstruction of *Romeria prima* by Clark and Carroll (1973) this feature is erroneously exaggerated and is actually not significantly different from that of *R. texana* and *Protocaptorhinus.* More notable, however, is the shorter length of the quadratojugals of *Romeria* and *Protocaptorhinus,* so that the length exceeds the height by no more than two and one half times. The quadratojugals of the protorothyridids tend to be more like those of the more primitive captorhinids. The straight occipital margin of the skull table of *Rhiodenticulatus,* seen also in *Protocaptorhinus,* is a derived feature with respect to the bilateral parietal embayment of the occipital margin of *Romeria* and the protorothyridids. On the other hand, *Rhiodenticulatus* is viewed as primitive with respect to the median embayment of the occipital margins of *Labidosaurus, Eocaptorhinus,* and *Captorhinus.*

Rhiodenticulatus exhibits at least two characters that link it with the more primitive captorhinids *Romeria* and *Protocaptorhinus,* and exclude it from the more advanced *Labidosaurus, Eocaptorhinus,* and *Captorhinus.* It has been noted by several authors (Clark and Carroll, 1973; Heaton, 1979) that in the evolution of the captorhinids there is

a marked trend toward relative widening of the postorbital region of the skull. In *Labidosaurus, Eocaptorhinus,* and *Captorhinus,* the postorbital lateral expansion of the skull becomes so pronounced that the lateral margin of the skull in dorsal view is noticeably concave, whereas in *Romeria, Protocaptorhinus,* and *Rhiodenticulatus* it is essentially straight. *Labidosaurus, Eocaptorhinus,* and *Captorhinus* are advanced over *Romeria, Protocaptorhinus,* and *Rhiodenticulatus* in exhibiting the shared derived feature of blunt (rather than sharply pointed) postcanine maxillary teeth (Olson, 1984).

Finally, there is one unique feature of *Rhiodenticulatus* with respect to all other single-tooth-rowed captorhinids which on first consideration seems unquestionably primitive, its possession of small premaxillary teeth of subequal size. In all captorhinids the premaxillary teeth exhibit a steady but dramatic increase in size anteriorly, with the anterior teeth reaching sizes equal to, or greater than, the maxillary canine. Though *Rhiodenticulatus* is like its protorothyridid predecessors in this character, implying a primitive state, the alternative interpretation that it represents an evolutionary reversal is argued below.

On the basis of the above character state analysis we conclude that the most plausible relationship of *Rhiodenticulatus heatoni* to other captorhinids is that depicted by the cladogram of Fig. 5 in which it is the primitive sister taxon to *Labidosaurus, Eocaptorhinus,* and *Captorhinus* (plus all other multiple-tooth-rowed forms). We recognize, however, that the cladogram possesses a few weaknesses. First, several of the nodes are defined by only a single character. Second, there are at least two notable contradictions between the cladogram and the character state analysis presented. Perhaps the most obvious is the possession by *Rhiodenticulatus* of small, subequal premaxillary teeth. The cladogram requires that this character be interpreted as the result of a secondary reduction in tooth size, or an evolutionary reversal, rather than more simply, as our character analysis implies, a primitive character. The likelihood that such an event occurred, however, seems very reasonable in light of the several derived modifications of the dentition of *Rhiodenticulatus* noted: 1) a single, extremely large canine, 2) reduction of the maxillary dentition to 11 teeth, 3) reduction in the number of precanines to two, and 4) reduction of the premaxillary dentition to three teeth. Of these, the first three are judged unique to *Rhiodenticulatus* among the single-tooth-rowed captorhinids, whereas the last also occurs in *Labidosaurus*. It should be noted here, however, that in our opinion it seems quite likely that the reduction in the number of premaxillary teeth to three in *Rhiodenticulatus* and *Labidosaurus* was achieved independently given the otherwise marked differences between their dentitions. A second possible inconsistency between the
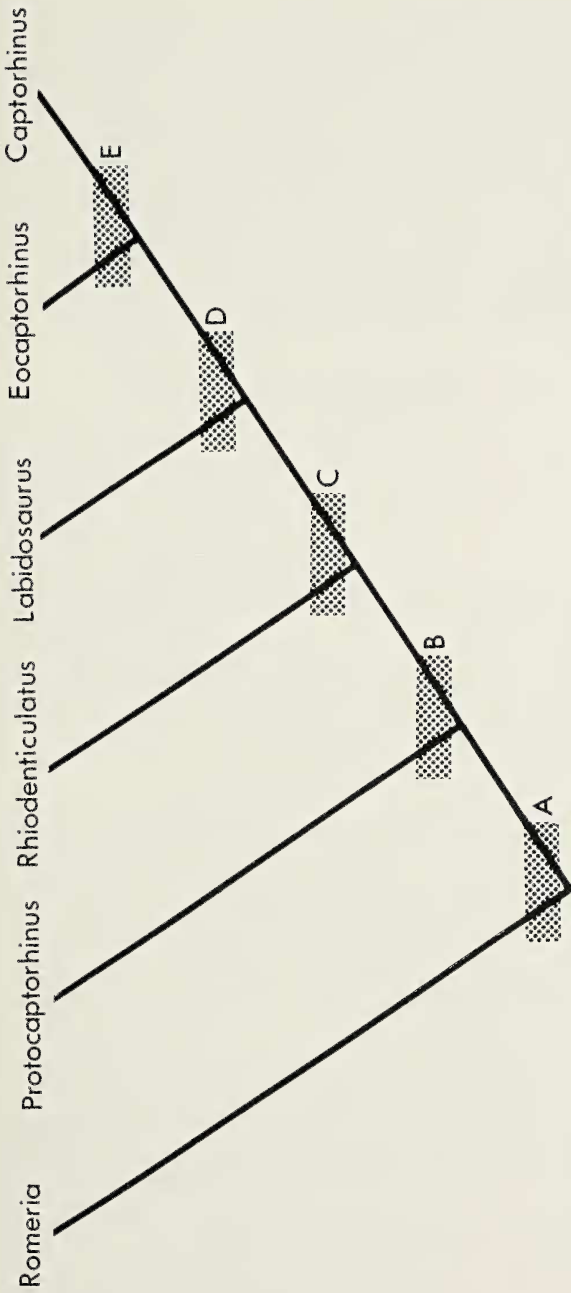
Fig. 5.—Cladogram illustrating possible relationships of *Rhiodenticulatus heatoni*. Shared derived characters: A, hooked premaxilla, loss of tabular, loss of ectopterygoid, supinator process of humerus absent, clavicle with thumb-like process, reduced dentition; B, straight occipital margin of skull table; C, elongate quadratojugal; D, retroarticular process present, median embayment of occipital margin of skull table, marked expansion of postorbital cheek region, blunt postcanines; E, anteroposteriorly elongate retroarticular process.

placement of *Rhiodenticulatus* in the cladogram and our character state analysis concerns the unique derived features of its dentition. If, as suggested above, the extremely large, single canine, 11 maxillary teeth, and two precanines of *Rhiodenticulatus* represent the most advanced stages of general trends within the single-tooth-rowed captorhinids, then it could be argued that these features indicate an advanced sister taxon relationship with *Labidosaurus* and *Eocaptorhinus* as well. This interpretation is rejected, however, in favor of the alternative argument that these unique features of the dentition of *Rhiodenticulatus,* as well as its relatively small, few premaxillary teeth, probably reflect an adaptation to a specialized diet not present in the other single-tooth-rowed captorhinids.

OTHER NEW MEXICO CAPTORHINIDS

In recent years the authors have collected additional captorhinid remains from the Lower Permian Cutler, Abo, and Sangre de Cristo formations at widely scattered localities in northern and central New Mexico. Although these specimens, as well as the two crushed and incomplete skulls referred to *"Puercosaurus obtusidens"* by Williston (1916), are too poorly preserved to be assigned safely to an existing taxon or made the basis of a new one, they permit the recognition of at least three possible morphotypes, one each from the Cutler, Abo, and Sangre de Cristo formations. These specmiens are, therefore, important as indicators of the diversity and spatial range of the captorhinids in the Lower Permian of New Mexico.

Indeterminate Cutler Captorhinid

All the indeterminate captorhinid specimens from Cutler Formation of the Rio Puerco drainage, Rio Arriba County, in the north-central part of the state are considered together as though pertaining to a single form distinct from *Rhiodenticulatus heatoni* of the same area. This is done despite the fact that the indeterminate specimens exhibit some differences from each other. It is realized that future discoveries may indicate that the differences between them may be due to either the presence of more than one undescribed species, or distinct growth stages of the same species, or both. If conspecificity is being masked by ontogenetic growth stages, then it is also conceivable that one or more of the indeterminate Cutler specimens may prove to be conspecific or congeneric with *R. heatoni.* This possibility is given some support by the presence in a few of the unassigned Cutler specimens of at least one feature considered derived in *R. heatoni,* the single, greatly enlarged canine. The unassigned Cutler specimens include:

FMNH 745, two crushed and very incomplete skulls referred to *"Puercosaurus obtusidens"* by Williston (1916), who illustrated only one, the same skull shown here in
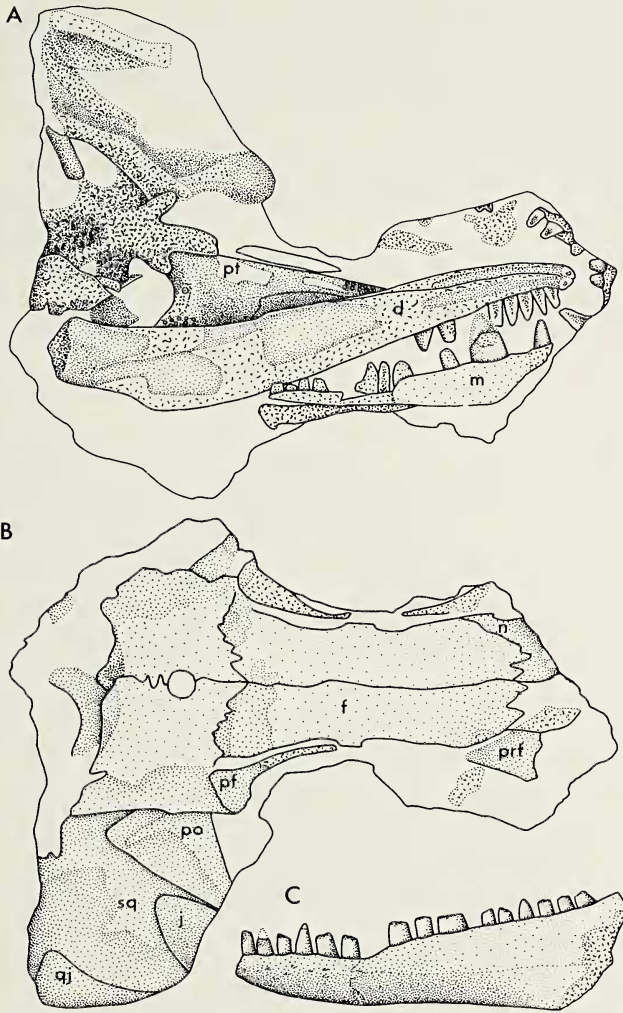
Fig. 6.—"*Puercosaurus obtusidens*" Williston (1916). A, dorsal, and B, ventral views of referred skull FMNH 745. C, lateral view of holotypic dentary FMNH 743. Abbreviations: d, dentary; f, frontal; j, jugal; m, maxilla; pf, postfrontal; po, postorbital; prf, prefrontal; pt, pterygoid; qj, quadratojugal; sq, squamosal. Scale = 1 cm.

Fig. 6A, B. Their exact locality is unknown, and according to Williston (1916) they were found by Mr. Miller in 1911 on the Rio Puerco a few miles below Arroyo de Agua. The holotypic left dentary of "*P. obtusidens*" (Fig. 6C) is too incomplete to assign to the Captorhinidae with reasonable certainty.
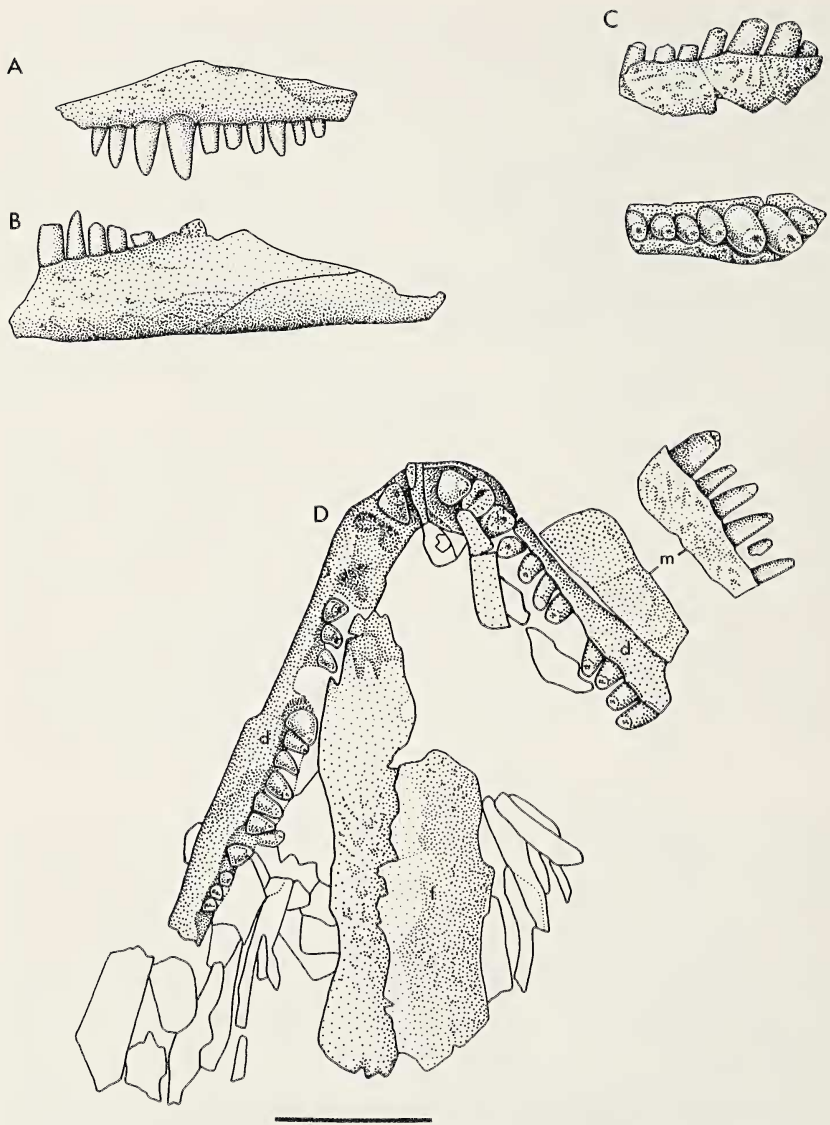
Fig. 7.—Indeterminate captorhinid from the Cutler Formation. A, lateral view of partial left maxilla, B, lateral view of posterior portion of left dentary, and C, lateral and dorsal views of anterior portion of right dentary of CM 28592. D, partial skull CM 28591 showing mainly paired frontals in dorsal view, dentaries in ventral view, and small portion of left maxilla in both medial and lateral views. Abbreviations: d, dentary; f, frontal; m, maxilla. Scale = 1 cm.

CM 28591, a partial skull (Fig. 7C, D); CM 28589, fourteen dorsal vertebrae, most of which are articulated in strings of two or three, and associated fragments of ribs and appendicular elements (Fig. 8A). These vertebrae are indistinguishable from those of *R. heatoni,* as are those of most captorhinids, but are included here because they were found in very close proximity to CM 28591 in NE¼SW¼NE¼ sec. 5, T. 22 N., R. 3 E. about 1.5 km northeast of Arroyo de Agua.

CM 28592, partial left maxilla (Fig. 7A), small portion of both dentaries (Fig. 7B), presacral vertebra, and left humerus (Fig. 8C). These elements undoubtedly belong to a single individual and were collected in N¼SW¼SE¼ sec. 8, T. 22 N., R. 3 E. about 1.6 km southeast of Arroyo de Agua.

The left premaxilla of the figured skull of FMNH 745 (Fig. 6) appears to have held four teeth as Williston (1916) described; this estimate takes into account an unoccupied space. The premaxillary teeth, as in *Rhiodenticulatus,* are very small relative to the pre- and postcanines of the maxilla. Accounting for spaces, the maxilla of FMNH 745 held approximately 13 to 15 teeth, including two or possibly three precanines, one extremely large canine, and 10 or 11 postcanines that decrease gradually in size posteriorly. As in *Rhiodenticulatus,* the basal diameter of the canine is about twice that of any of the postcanines. The dentition of the partial left maxilla of CM 28592 (Fig. 7A) is considerably different, however, in that the canine is relatively smaller when compared to the postcanines, and the third or posteriormost precanine is nearly as large as the canine, producing a double canine appearance. A segment of the right maxilla of CM 28591 (Fig. 7D) shows the canine as dominating the postcanines in size, though not as greatly as in *Rhiodenticulatus.* The maxillary dentitions of FMNH 745, CM 28591, and CM 28592 are single rowed, and the teeth appear as simple, sharply pointed pegs except for a slight, posterior curvature of the tips. The frontals of FMNH 745 and CM 28591 (Figs. 6B, 7D) are complete, and their very narrow contribution to the orbital rim is clearly discernable. As in *Rhiodenticulatus,* the portion of frontal anterior to its contribution to the orbital rim is considerably larger than that which is posterior. In FMNH 745 the pineal foramen appears to be more centrally positioned along the median parietal suture than in *Rhiodenticulatus.* The dentary dentition is well preserved in CM 28591 except for most of the teeth lacking their tips; the more complete right dentary is estimated to have held about 18 teeth. The first tooth is extremely small in typical captorhinid fashion, the second and third are subequal in size and much larger than the others of the series, and the following teeth do not exhibit an obvious size pattern except for the last three being greatly reduced. The anterior seven teeth preserved on the fragment of right dentary of CM 28592 (Fig. 7C) exhibit the same size relationships as in CM 28591. In contrast, the first five teeth of the left dentary of the FMNH 745 are of subequal, moderate size. The dentary teeth also have the form of simple, sharply pointed pegs.
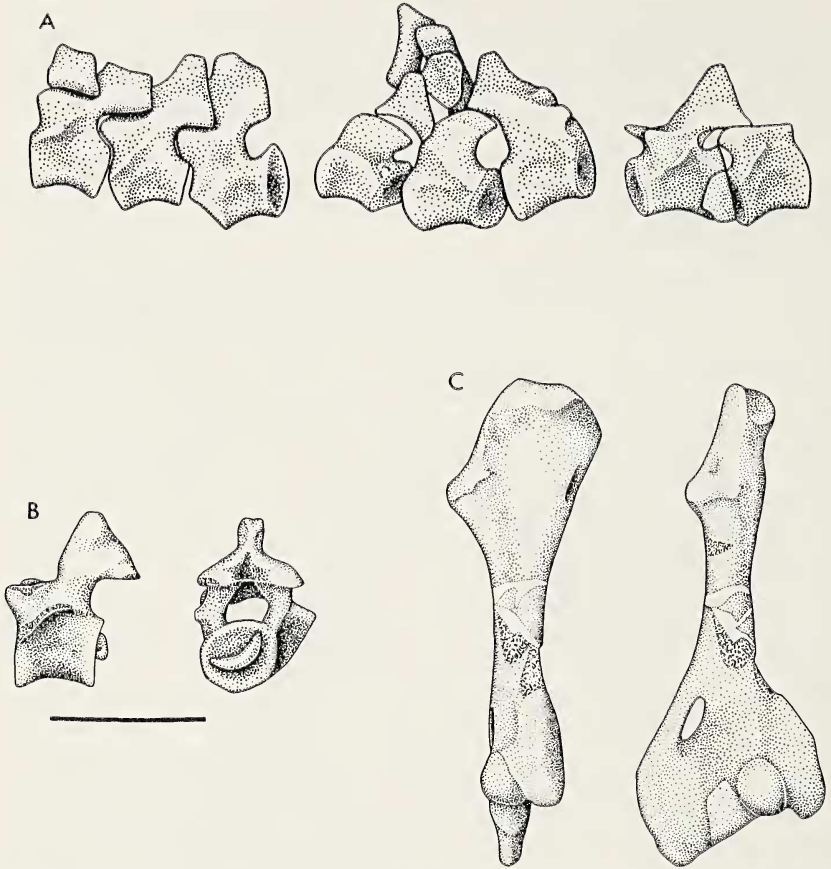
Fig. 8.—Indeterminate captorhinid from Cutler Formation. Presacral vertebrae of A, CM 28589, and B, CM 28592. C, dorsal proximal and distal ventral views of left humerus CM 28592. Scale = 1 cm.

The presacral vertebrae of CM 28589 and CM 28592 (Fig. 8A, B) are alike and as far as comparisons will allow like those of *Rhiodenticulatus*. The neural spine is small, triangular in lateral view, and distinctly set off from the neural arch, which has the expected swollen appearance. The zygapophyses extend slightly beyond the lateral margins of the centra, and their articular facets are essentially horizontal. There is no evidence of a suture between the neural arch and centrum. The transverse process is positioned on the anterodorsal quadrant of the lateral surface of the centrum. In lateral view the process is a thin, ridge-like structure whose base extends anteroventrally to the centrum
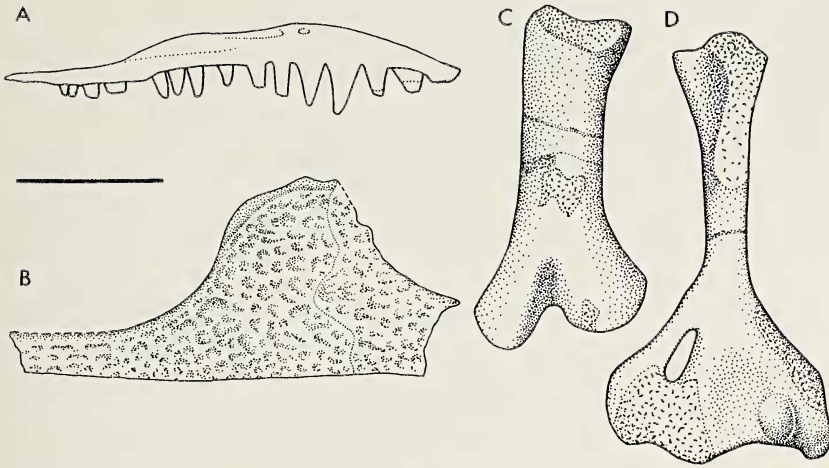
Fig. 9.—Indeterminate captorhinid CM 41707 from the Abo formation. A, medial view of left maxilla, B, lateral view of left jugal, C, dorsal view of distal half of right femur, and D, distal ventral view of left humerus. Scale = 1 cm.

rim. In anterior view its lateral projection diminishes as it extends to the centrum rim, giving it a wing-like appearance. The ends of the centra are beveled slightly so as to give them a slightly keystone appearance in lateral view. The lateral surfaces of the centra are moderately concave in horizontal section, producing a spool-shaped appearance. The only clearly visible intercentrum is seen in the vertebra of CM 28592 (Fig. 8B); it has a low, narrowly triangular outline in lateral view and a crescent-shaped outline in anterior view.

The only appendicular element of the indeterminate specimens from the Cutler Formation worthy of description is the well preserved left humerus of CM 28592 (Fig. 8C). It differs from those of *Eocaptorhinus* and *Captorhinus* (Holmes, 1977) mainly in having a more gracile form, but in this feature is also like that of *Rhiodenticulatus*. The proximal and distal ends are relatively narrower, and the entepicondyle extends far more distally beyond the radial condyle than in *Eocaptorhinus* or *Captorhinus*.

Indeterminate Abo Captorhinid

A second possible New Mexico captorhinid form for which there is insufficient morphological information to assign to either an existing or a new taxon is based on a single specimen, CM 41707, collected from the Abo Formation about 20 km northeast of Socorro in the central part of the state in SE¼NE¼W¼ of sec. 14, T. 2 S., R. 3 E. CM

41707 consists of disarticulated elements of the skull and postcranial skeleton of an individual that are randomly associated and densely concentrated in a small, strongly indurated, red concretion. Only those elements close to the outer surface of the concretion were prepared and include: a left maxilla, left jugal, anterior half of the right mandible, a presacral vertebra, ribs, greater part of the left humerus, distal half of right femur, and several unidentified fragments. Only a few of the above elements are figured here (Fig. 9). The left maxilla (Fig. 9A), although poorly preserved, retains an accurate outline of its dentition, which consists of 14 teeth and at least one unoccupied space; in this feature it is like the maxilla of the indeterminate Cutler specimen FMNH 745. As in *Rhiodenticulatus*, there are two moderate sized precanines. Although the third tooth is the largest of the series and should be considered a canine, the fourth tooth is nearly as large, giving CM 41707 a distinctly double canine appearance like that in the partial left maxilla of the indeterminate Cutler specimen CM 28592. The basal diameter of neither canine of CM 41707, however, exceeds that of the largest postcanine as greatly as does the single, enlarged canine of *Rhiodenticulatus*. The teeth gradually decrease in size from the first canine to the seventh tooth; this is followed first by four somewhat larger, subequal teeth and then by the last three and smallest teeth of the series. The jugal (Fig. 9B) is like that of other captorhinids. A smooth flange on the dorsal margin of the posterior plate clearly indicates the position of the overlaping postorbital, and the spike-like projection on the posterior margin marks the point of separation between the jugal-squamosal and jugal-quadratojugal contacts.

The anterior half of the right mandible (not figured) is exposed in lateral and dorsal view, and the first 16 teeth are present, though many are represented by only their bases. As in the captorhinids *Eocaptorhinus* and *Captorhinus*, the first tooth is extremely small, the second moderate sized, and the third is greatly enlarged and dominates the entire series, having a basal diameter of about 2 mm and a height of about 5 mm. The fourth tooth is the second largest of the series, with a basal diameter of about 1.5 mm and an estimated height of 2.5 mm, whereas the fifth is greatly reduced and about equal to the second in size. Teeth 6, 7, and 8 are of subequal, moderate size, the larger ninth tooth appears to have been about the size of the third tooth, and the remaining seven teeth steadily decrease in size posteriorly. All the dentary teeth appear to have the form of simple pointed pegs and are aligned in a single row. As in *Eocaptorhinus* and *Captorhinus*, the first three teeth lean obliquely forward and the fourth is nearly vertical. The one partial vertebra appears to be typical of captorhinids. The left humerus of CM 41707 (Fig. 9D) is nearly complete, missing only a
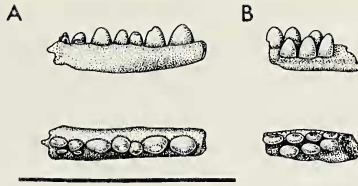
Fig. 10.—Indeterminate captorhinid from the Sangre de Cristo Formation. Lateral and ventral views of maxillary fragments A, CM 28594, and B, CM 28595. Scale = 1 cm.

portion of its proximal end. The shaft is more slender and the entepicondyle possibly less expanded than those of *Eocaptorhinus* or *Captorhinus*. The entepicondyle extends distally only slightly beyond the radial condyle. In contrast, the distal half of the right femur (Fig. 9C) is very stoutly constructed, especially in comparison with *Eocaptorhinus* and *Captorhinus*.

Indeterminate Sangre de Cristo Captorhinid

Numerous fragments of captorhind maxillae and dentaries have been collected from the Lower Permian Sangre de Cristo Formation approximately 50 km southeast of Santa Fe in the northeastern part of the state in NE¼ sec. 36, T. 14 N., R. 13 E. Two of the maxillary fragments are figured (Fig. 10), and they clearly indicate that the captorhinid from this locality had at least two rows of teeth. In one (CM 28594, Fig. 10A) the broken edges of a second row of teeth can be seen lateral to the posterior end of the main row. Medial wear facets of the teeth, which are more evident on the other fragment (CM 28595, Fig. 10B), give them the same blunt, peg-like outlines seen in *Eocaptorhinus* and multiple-tooth-rowed forms such as *Captorhinus*. These two features of the dentition indicate clearly that the Sangre de Cristo captorhinid remains are of a distinct and more advanced taxon than the other representatives of the family in New Mexico.

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